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Local epiphyte establishment and future metapopulation dynamics in landscapes with different spatiotemporal properties

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Abstract. Understanding the relative importance of different ecological processes on the metapopulation dynamics of species is the basis for accurately forecasting metapopulation size in fragmented landscapes. Successful local colonization depends on both species dispersal range and how local habitat conditions affect establishment success. Moreover, there is limited understanding of the effects of different spatiotemporal landscape properties on future metapopulation size. We investigate which factors drive the future metapopulation size of the epiphytic model lichen species *Lobaria pulmonaria* in a managed forest landscape. First, we test the importance of dispersal and local conditions on the colonization–extinction dynamics of the species using Bayesian state-space modelling of a large-scale data set collected over a 10-yr period. Second, we test the importance of dispersal and establishment limitation in explaining establishment probability and subsequent local population growth, based on a 10-yr propagule sowing experiment. Third, we test how future metapopulation size is affected by different metapopulation and spatiotemporal landscape dynamics, using simulations with the metapopulation models fitted to the empirical data. The colonization probability increased with tree inclination and connectivity, with a mean dispersal distance of 97 m (95% credible intervals, 5–530 m). Local extinctions were mainly deterministic set by tree mortality, but also by tree cutting by forestry. No experimental establishments took place on clearcuts, and in closed forest the establishment probability was higher on trees growing on moist than on dry-mesic soils. The subsequent local population growth rate increased with increasing bark roughness. The simulations showed that the restricted dispersal range estimated (compared to non-restricted dispersal range), and short tree rotation length (65 yr instead of 120) had approximately the same negative effects on future metapopulation size, while regeneration of trees creating a random tree pattern instead of an aggregated one had only some negative effect. However, using the colonization rate obtained with the experimentally added diaspores led to a considerable increase in metapopulation size, making the dispersal limitation of the species clear. The future metapopulation size is thus set by the number of host trees located in shady conditions, not isolated from occupied trees, and by the rotation length of these host trees.

Key words: Bayesian model; colonization; dynamic landscapes; extinction; host tree; lichen; scenario; state-space; tree rotation.

INTRODUCTION

Metapopulation theory has been successfully applied to predict the occupancy, colonization and extinction of a wide range of species (Hanski and Gaggiotti 2004, Hanski 2005). Species forming metapopulations naturally go extinct from and re-colonize their habitat patches (Hanski and Gaggiotti 2004). If the colonization rate exceeds the extinction rate, the metapopulation will persist (Hanski 1999). For species whose metapopulation dynamics are slow, the spatiotemporal dynamics of the patches also have large effects on metapopulation size (e.g., Fahrig 1992, Keymer et al. 2000, Wilcox et al. 2006).

Theoretical and observational studies have suggested that successful colonization depends on the dispersal

ability of the species, connectivity to patches and local habitat conditions (Hanski 1999, Fleishman et al. 2002, Snäll et al. 2005a). Colonization includes the two steps of dispersal and establishment, where dispersal is the ability of the propagules to arrive at potential recruitment sites (Eriksson and Ehrlén 1992, Nathan and Muller-Landau 2000), and establishment is determined by the availability of microsites with suitable conditions necessary for germination and propagule survival (Harper 1977, Nathan and Muller-Landau 2000). Because both dispersal and establishment limitations are key components of the colonization process, both should influence metapopulation dynamics (Hanski and Gaggiotti 2004). There is extensive evidence for the effect of connectivity on colonization, with a higher proportion of individuals reaching a patch within short distances from sources due to restricted dispersal range (Hanski 1999). These studies invoke propagule dispersal range as the explanation for distance-dependent patterns, but are inherently limited in their ability to

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distinguish the influence of dispersal range from that of environmental control (Smith and Lundholm 2010). Moreover, observational seed-sowing experiments have shown that recruitment of seedlings is a decisive step during the early phase of establishment (Nathan and Muller-Landau 2000, Clark et al. 2007). However, these studies include seed limitation (e.g., seed density) as surrogate for dispersal and do not include any link to empirically measured dispersal range (Robledo-Arnuncio et al. 2014). We are not aware of any studies testing both the importance of dispersal range and establishment limitation on metapopulation dynamics, and which factors explain the establishment and subsequent local population growth of any sessile species.

Local extinctions may result from either demographic or environmental stochasticity in intact patches or from patch destruction (Thomas 1994, Snäll et al. 2003). According to theory, if population extinctions are mainly stochastic, then the extinction risk is negatively related to patch area (Hanski 1999). If, on the other hand, the metapopulation dynamics are considerably slower than the turnover rates of the patches, local extinctions occur deterministically and are driven by patch destruction (Snäll et al. 2003). However, the empirical evidence for this hypothesis is limited. For example, some studies have shown intermediate extinction dynamics in sessile organisms with both stochastic and deterministic extinctions (Laube and Zotz 2007, Caruso et al. 2010, Öckinger and Nilsson 2010, Fedrowitz et al. 2012, Zartman et al. 2012). Distinguishing between the relative importance of stochastic and deterministic extinctions is important, as failing to do so may overestimate future metapopulation size (Snäll et al. 2005a, Hodgson et al. 2009).

To date, most metapopulation studies have considered metapopulation dynamics in static landscapes, i.e., habitat patches are permanently present (Johst et al. 2011). Studies that incorporate both metapopulation and landscape dynamics are mostly theoretical, while empirical metapopulation studies in dynamic landscapes are scarce (Van Teeffelen et al. 2012). The theoretical work has suggested that temporal landscape properties affect species persistence more than spatial ones (Fahrig 1992). Indeed, the rate of habitat destruction may influence species persistence regardless of the amount of habitat available (Keymer et al. 2000). Furthermore, although species persistence is influenced by the rate of patch creation (Wilcox et al. 2006), persistence is more effectively increased by reducing the rate of patch destruction than by increasing the rate of patch creation (Johst et al. 2011). This theoretical work constitutes the basis for the empirical work and provides qualitative recommendations, but empirical work is required to provide quantitative evidence for a range of species relative to different landscape dynamics (Fahrig 1992, Wilcox et al. 2006, Van Teeffelen et al. 2012).

Epiphytes and their host trees provide an excellent model system to test theory on metapopulation dynamics of sessile species in dynamic landscapes. An epiphyte grows non-parasitically upon, or attached to a living tree,

shrub or other vegetation (Barkman 1958). Their long-term dynamics are influenced by spatial as well as temporal landscape attributes (Snäll et al. 2005b, Fedrowitz et al. 2012, Johansson et al. 2013). Colonizations are affected by connectivity as well as local patch conditions (e.g., Snäll et al. 2005a). They are long-lived organisms with potentially both stochastic and deterministic extinctions, as their patches are destroyed when the occupied tree falls. However, the relative importance of factors influencing the probability of colonization and extinction, and how these influence the future metapopulation size, remains unclear.

Here, we use a large-scale data set collected over a 10-yr period to estimate the relative importance of factors influencing future metapopulation size of an epiphytic lichen in a managed forest landscape. Our model species is the well-studied epiphytic lichen *Lobaria pulmonaria*. First, we test the importance of dispersal range, local factors and tree fall on the colonization-extinction dynamics of the species using observational data. Second, we test the importance of restricted dispersal range and propagule availability on establishment probability. This is based on recruitment success 10 years after diaspores were experimentally transplanted on unoccupied but presumably suitable trees in our study landscape. This includes estimating the relative importance of local factors on propagule establishment and subsequent local population growth. Third, we test how the future *Lobaria pulmonaria* metapopulation size is affected by different metapopulation and landscape dynamics in terms of spatial tree regeneration pattern and tree rotation length. This is conducted using simulations with metapopulation models fitted to the empirical data.

MATERIALS AND METHODS

The model species

The model species is *Lobaria pulmonaria*, an epiphytic lichen. It is widespread throughout the northern hemisphere, but has declined considerably over the last century due to intensive forest management and air pollution (Smith et al. 2009, Artdatabanken 2015). It is an indicator for clean air and undisturbed forests (Kuusinen 1996) and is considered a flagship and an umbrella species for nature conservation, since it is easy to identify, occurs in old forests and is associated with other red-listed species (Scheidegger and Werth 2009). In the boreal region, it is confined to aspen (*Populus tremula*) and goat willow (*Salix caprea*) (Kuusinen 1996). It disperses asexually with soredia, isidia, or thallus fragments (Jørgensen et al. 2007), and sexually by spores forming in apothecia (Denison 2003). Previous studies have suggested both restricted (Walser et al. 2001, Walser 2004, Snäll et al. 2005b), and rare long-distance dispersal (Werth et al. 2006, Gjerde et al. 2015). However, the studies are based on occurrence pattern data or small-scale dispersal distance experiments. Here, we use large-scale data on

colonization and extinction dynamics and an establishment experiment over ten years.

Study landscape and empirical colonization-extinction data

The study was conducted in a 50-km² landscape in central-eastern Finland. The intensively managed boreal forest (Appendix S1: Fig. S1) is dominated by spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), birch (*Betula* spp.), and intermingled aspen (*Populus tremula*) and goat willow (*Salix caprea*).

In 1997–2000, all 3,526 aspens (≥ 15 cm in diameter at breast height [dbh]; 2,002 trees) and goat willows (≥ 10 cm dbh; 1,524 trees) were mapped and the occurrence of *L. pulmonaria* on each tree was surveyed (Gu et al. 2001). In 2008–2010, species occurrence was surveyed again on the same trees. This included registering tree fall or tree cutting by forestry. Colonization was defined as species absence on the tree in the first survey and presence in the second survey. Extinction was defined as species presence on the tree in the first survey and absence in the second. Extinctions were either deterministic resulting from tree fall (naturally or cut), or stochastic from standing, living trees.

For each tree in the second survey, we recorded the environmental variables alive or dead, dbh, depth of bark crevices (in mm, 50 cm above the ground), percentage of bark cover of the trunk, and tree inclination (from vertical). We recorded soil moisture and degree of shade as detailed in Anonymous (1997) and Snäll and Jonsson (2001). Soil moisture within 2 m radius zone around each tree was classified as either dry-mesic (ground water level > 1 m below the soil surface) or mesic-moist (ground water level < 1 m below the soil surface). Degree of shade was classified as sun exposed (fully sun exposed during 50–100% of the day) or shaded (in one-half total shade most of the time).

In order to estimate species detectability, we conducted repeat visits to trees during the second survey. For obtaining a large sample size, this work was conducted in both the managed study landscape (Appendix S1: Fig. S1) and the old-growth landscape studied in Snäll et al. (2005b).

The establishment experiment

The experiment was established in 2004. *Lobaria pulmonaria* thalli rich in the asexually reproducing diaspores soredia and isidia were collected in the study region. The thalli were air dried and the diaspores were brushed off from the thallus surface. In the evening before the sowing, the diaspores were poured into water and the diaspore concentration was determined based on counting them in a counting chamber following the principles of Sundberg and Rydin (1998). The resulting concentrations used in different establishments were 6,800–9,200 diaspores/mL.

The diaspore solutions were sprayed using a syringe on aspens and goat willows in nine forest stands representing typical age and soil types in managed boreal landscapes: closed forest on dry, mesic, and moist soil types and

clear-cut forest on mesic soil. The forest stands were selected randomly, with the restriction that they should be located < 600 m from a forest road. Within each stand, non-occupied trees mapped in the first survey were randomly selected in different dbh classes (10–52 cm). On each tree, 1 mL of diaspore solution was sprayed onto the bark at 1.5 m height at the aspects north, south, east, and west. A total of 99 trees were inoculated. In 2014, we recorded *L. pulmonaria* establishment and performed thallus counts.

Statistical modelling and model building

We fitted a Bayesian spatially explicit model (Gelman et al. 2004) for landscape-scale epiphyte colonization–extinction in 10-yr time steps using the 2,055 trees that were living and with 100% bark cover in the second survey (Appendix S2). We thus assumed that the epiphytic species does not colonize the trees that were dead in the first survey or had died or fallen between the surveys (3,526 minus 2,055 trees). It is a state-space model accounting for detectability (MacKenzie et al. 2003) and including an offset for the varying time steps between the surveys (9–13 yr). The model building included testing the effects of the explanatory variables on colonization.

We evaluated the models based on biological plausibility of the posterior distribution of the parameters and model deviance, as the use of DIC is not appropriate for mixture/hierarchical models (Hooten and Hobbs 2015). We first fitted a null model not including any explanatory variables (Appendix S2: Eqs. S1–S4). We then fitted models with spatial connectivity with one or two dispersal range parameters (Appendix S2: Eqs. S5, S6). Next we extended the spatial model with single non-spatial variables (Appendix S2: Eq. S5). The lowest deviance among these models was much higher than the deviance of the model including only spatial connectivity. However, for models including inclination, the probability of the slope parameter β_1 being greater than zero was large. Therefore, the final model reported includes inclination as a variable.

In a separate analysis of the establishment experiment, we jointly tested which environmental variables explained the probability of establishment and thallus counts using a zero-inflated model (Zeileis et al. 2008, Paltto et al. 2011). Zero-inflated models are two-component mixture models in which zeros can result from each of two processes; here, the establishment process (modelled with a binomial error distribution and a logit link function) and the abundance process (modelled with a negative binomial error distribution, to account for over-dispersion, and a log link function). We used forward stepwise model selection based on likelihood ratio tests to determine which covariates should be included in the two components of the model. The null model thus had only an intercept for each of the two components. We first performed model selection for the thalli counts component and then for the establishment component conditional on

the model selected for the thalli counts. Doing selection the other way around led to convergence problems. Modelling was performed at the tree level, aggregating the data from the four inoculated aspects per tree on the total of 99 trees with diaspore inoculation. In the count (sub-) models, we accounted for the varying diaspore concentrations applied on different trees by including the log of the diaspore concentration as an offset variable.

The Bayesian colonization–extinction models were fitted using Openbugs 3.2.3 rev. 1012 (Thomas et al. 2006). Two chains of 40,000 iterations were thinned by 10 after a burn-in of 10,000 iterations. The software R version 3.1.1 (R Development Core Team 2014) was used to simulate the scenarios (see *Simulated scenarios*), and also to fit the zero-inflated model with the add-on library *pscl* 1.4.9, and the add-on library *lme4* 0.9–34 to compute the likelihood ratio tests.

Simulated scenarios

The scenarios aimed at testing the effects of different key components of metapopulation dynamics in dynamic landscapes on future metapopulation size (Hanski 1999, Keymer et al. 2000, Snäll et al. 2003, Wilcox et al. 2006, Johst et al. 2011): What is the support for the effect of restricted dispersal range (three dispersal functions tested), local stochastic extinctions, rate of patch destruction, and pattern of patch creation? We simulated nine scenarios with different *L. pulmonaria* metapopulation dynamics and tree dynamics among 2,431 host trees (Table 1) using the models in Appendix S2 and parameter estimates in Appendix S3: Table S1.

The three dispersal models investigated were the (1) mean non-spatial colonization rate, spatial colonizations dependent on connectivity modelled with one (2) or two (3) parameters (the latter modelling long-distance dispersal, Appendix S2: Eq. S6). In one scenario (S3; Table 1) we used the raw establishment rate given by the field

experiment. Moreover, we used either the mean stochastic extinction rate, or zero stochastic extinction. For tree fall, we used either the rate 1/6.5 or 1/12.0 decades. The higher rate corresponds to the minimum allowed forest rotation length in northern Sweden by law (65 yr). The lower rate corresponds to the typical northern Swedish rotation length since the clear-cutting forestry started in the 1950s (100–120 yr; Fries et al. 2015), and assumed long rotation length in Finland (Mönkkönen et al. 2014). We further assumed that regenerated trees either appeared at the same location as where a tree had just fallen, thus retaining the aggregated tree pattern, or at a random location within the landscape (Appendix S1: Fig. S1). As future intensified forestry may result in both lower host tree density and less aggregated tree patterning, we contrasted the current aggregated pattern against a random regeneration scenario. We kept the total tree numbers constant by directly replacing a fallen tree with a new tree suitable for colonization. However, since the scenarios focused on metapopulation and tree dynamics and we do not have a model for tree inclination dynamics, we made simulations with models not including this variable (inclination).

We simulated each scenario using 1,000 draws from the joint posterior probability distributions of the model parameters (Appendix S3: Table S1). As a test for difference between scenarios, we calculated the support that the predicted distribution in metapopulation size in year 100 was lower in scenarios two to nine (S2–S9) than in the base scenario one (S1, Table 1).

RESULTS

Colonization–extinction dynamics

During the 10-yr period, we recorded 11 colonizations events of *L. pulmonaria* among the 1,997 trees that were unoccupied in the first survey and still standing and vital in the second one. The detectability was $172/180 = 0.956$:

TABLE 1. Simulated scenarios with different models of colonization, extinction, host tree rotation length, and spatial pattern of tree regeneration.

Scenario	Colonization	Extinction	Rotation length (yr)	Regeneration	Probability < S1
S1	non-spatial†	mean‡	120	at tree fall	
S2	non-spatial†	0	120	at tree fall	0.47
S3	experimental§	mean‡	120	at tree fall	0
S4	spatial¶	mean‡	120	at tree fall	0.77
S5	spatial¶	mean‡	120	random	0.86
S6	non-spatial†	mean‡	65	at tree fall	0.96
S7	spatial¶	mean‡	65	at tree fall	0.94
S8	spatial¶	mean‡	65	random	0.98
S9	spatial, with γ #	mean‡	65	random	0.97

Note: Also shown are results on the probability that the metapopulation size is smaller in year 100 than in scenario S1.

† Appendix S2: Eqs. S3 and S5 but lacking the term $\log(K_i)$.

‡ Appendix S2: Eq. S4.

§ Experimental establishment rate, 8/99.

¶ Appendix S2: Eqs. S3, S5 and S6, with γ fixed at 1.

Appendix S2: Eqs. S3, S5 and S6.

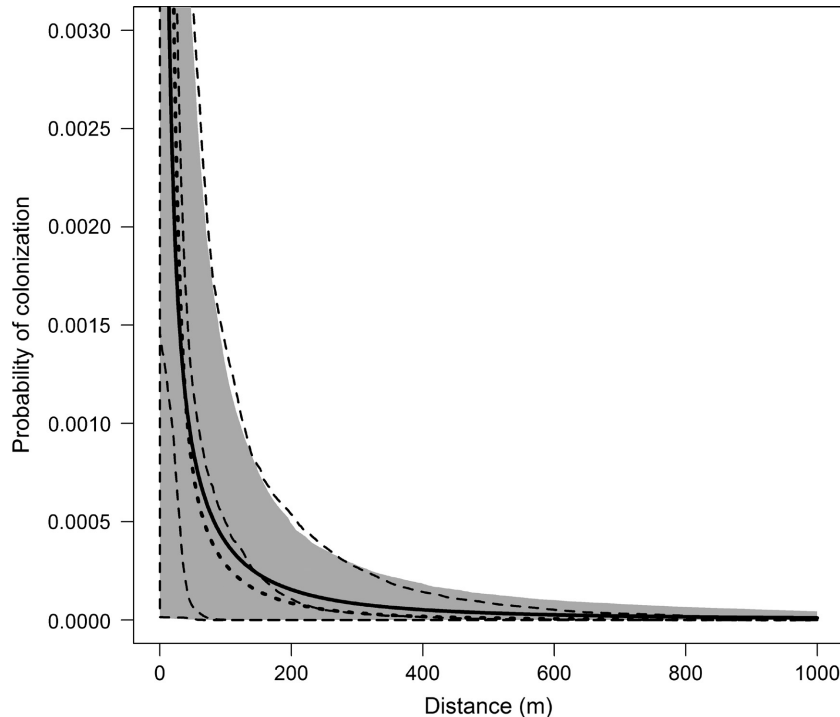


FIG. 1. Colonization functions of *Lobaria pulmonaria*. The dashed lines show the 95 and 50 highest predictive posterior density percentiles, respectively, using the model including only α . The gray polygon shows the 95 highest predictive posterior density percentiles using the model including the parameters α and γ . The heavy lines show the mean colonization probability using models with either only α (dotted), or both α and γ (solid).

the species was detected on 172 of the 180 trees known to be occupied. Model deviance was reduced when changing the non-spatial model (mean deviance = 6127) to be spatial by adding the dispersal parameter α (6106), but not when also adding the parameter γ (6112). In the models with only single explanatory variables, we found strong support for a positive effect of inclination, as judged by a 99% probability that β_1 was >0 (i.e., $\Pr(\beta_1 > 0) = 0.99$). We therefore retained inclination in the final model ($\Pr(\beta_1 > 0) = 0.82$), where the mean dispersal range ($1/\alpha$) was 97 m (mode; lower and upper 2.5% percentiles: 5, 530; Fig. 1; Appendix S3).

We recorded 39 extinctions events among the 131 trees that were occupied in the first survey (totally 3,526 trees). Of these, 18 trees had fallen and 13 had been cut by forestry, three were dead, snags (i.e., the high stump remaining after the tree top has fallen off) or had bark starting to fall off, and five were vital trees (i.e., with stochastic extinctions). The deterministic extinction rate was thus $(18 + 13 + 3)/131 = 0.260$. The lower stochastic extinction rate $5/(131 - 18 - 13 - 3) = 0.052$ from vital trees over a 10-yr period gives an average local population longevity of $10 \text{ yr} \times 5/(131 - 18 - 13 - 3) = 194 \text{ yr}$.

Dispersal vs. establishment limitation

The probability of establishment was 14.7 times higher 10 years after a total of 27,200–36,800 diaspores were

sprayed on the four aspects of each tree; *L. pulmonaria* had established on eight of the 99 experimental trees (8.1%, on one or two aspects per tree). More specifically, 283 thalli had emerged from a total of 782,936 diaspores added, meaning a 36×10^{-5} probability of establishment per diaspore. No establishments were recorded on trees in sun-exposed conditions or on dry soils. The establishment probability was six times higher on moist-wet compared to dry-mesic soils ($P = 0.02$), and the subsequent local population growth increased with increasing depth of bark crevices ($P = 0.02$). For further details, see Table 2.

Future metapopulation size

The simulated scenarios using the colonization-extinction models revealed clear effects of propagule availability, restricted dispersal range, and tree rotation length and regeneration pattern on future metapopulation size (Fig. 2, Table 1). The base scenario assuming non-spatial mean colonization-extinction dynamics and long rotation length (S1) projected stable metapopulation size. This conclusion was not changed when assuming zero stochastic extinction rate (S2). However, the scenario assuming the best-fitting model with restricted dispersal range (S4), including that trees regenerate at random locations (S5), projected smaller mean metapopulation size (77–86% support, Table 1) compared to assuming non-spatial

TABLE 2. Zero-inflated count regression models explaining establishment probability and number of thalli of *Lobaria pulmonaria* on 99 inoculated trees.

Response variables and explanatory variables†	Parameter estimate	Standard error‡	Test statistic (z values)§	P§
Count model				
Intercept	-8.42	1.13	-7.45	<0.001
Bark roughness	0.21	0.09	2.41	0.02
$\phi\parallel$	-0.54	0.77	-0.70	0.48
Binomial model‡				
Intercept	-5.70	0.76	-7.52	<0.001
Soil moisture	-1.98	0.86	-2.29	0.02

† $R^2 = 0.58$.

‡ The probability of non-occurrence. Hence, the interpretation of the signs of the estimates is the opposite of typical binomial models.

§ The z values for non-occurrence models and associated P values.

¶ ϕ is a parameter of the negative binomial variance function (Zuur et al. 2009).

dynamics (S1). In the scenarios with random regeneration (S5, S8), the final mean metapopulation sizes were 80% and 68% of sizes in the scenarios with replacement regeneration (S4, S7), respectively. In the scenario assuming the raw experimental propagule establishment rate (S3), almost 50% of the trees had become occupied after 100 yr (inset Fig. 2). In contrast, decreasing the rotation length

from 120 to 65 yr (S6–S8) clearly further reduced the future metapopulation size compared to S1, with a support of 96–98%. The support was highest when using the best-fitting model with restricted dispersal range and random location of regenerated trees. This conclusion was unchanged when using the spatial model with two parameters explicitly modelling long-distance dispersal (S9).

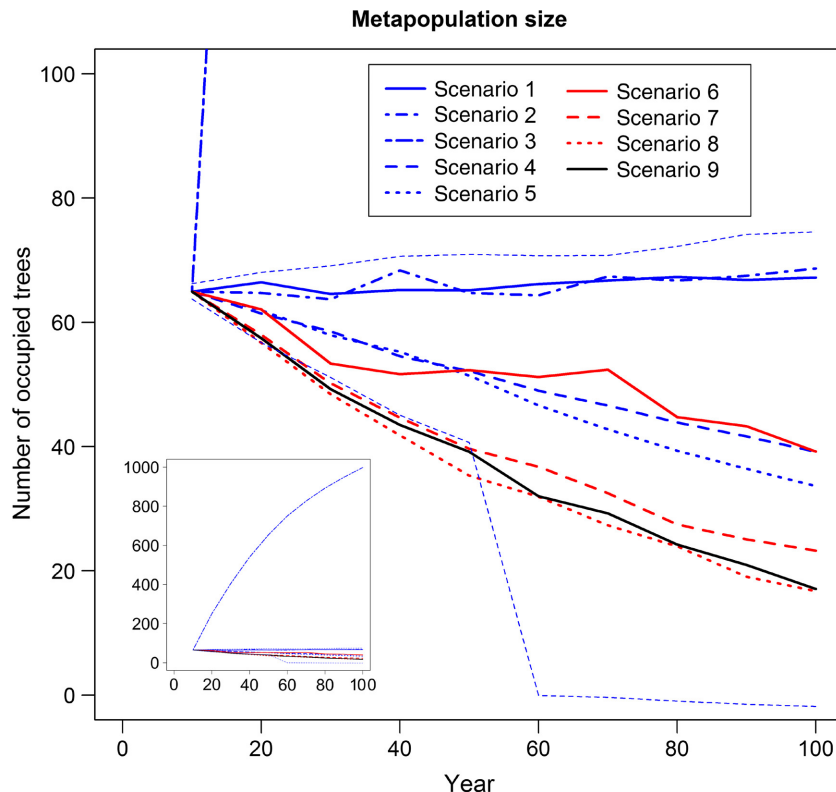


FIG. 2. Projected number of trees occupied by *Lobaria pulmonaria* among 2,431 trees in scenarios of different metapopulation and host tree dynamics (Table 1). The scenarios differ in terms of rates of *L. pulmonaria* colonization, extinction, and spatiotemporal dynamics of the host trees. The lines show the mode of the projection density interval. Shown are also the limits of the 95% highest projection density interval for Scenario 4 for illustration of uncertainty (thin, dashed, blue lines). The inset figure only has different y-axis limits and illustrates the scenario using the experimental establishment rate (Scenario 3).

DISCUSSION

We combined large-scale observational and experimental data sets on metapopulation dynamics and local establishment with projection simulations of a sessile species confined to dynamic habitat patches. We found that propagule availability and restricted dispersal range limited the colonization rate, and both factors were important predictors of future epiphyte metapopulation size in fragmented landscapes. Restricted dispersal range explained why the colonization rate increased with increasing connectivity to occupied trees. Moreover, local habitat conditions affected both propagule establishment and subsequent local population growth. Local extinctions were driven by patch destruction and thus stochastic extinctions were negligible for projecting future metapopulation size. Additional landscape drivers of future metapopulation size were, in particular, the tree rotation length, but also the aggregation of host trees.

Our results confirm that propagule availability limits the colonization rate of epiphyte metapopulations and is an important predictor of future metapopulation size. The colonization rate greatly increased with propagule addition (by a factor of 15), suggesting dispersal limitation due to the failure of propagules to arrive at potential recruitment sites (Eriksson and Ehrlén 1992, Nathan and Muller-Landau 2000). This is in agreement with previous experimental seed addition studies, which have shown that recruitment was mainly limited by propagule availability rather than microsite availability in grassland communities (Tilman 1997, Zobel et al. 2000, Foster and Tilman 2003, Poulsen et al. 2007). They showed that propagule addition led to higher recruitment in unsaturated plant communities that contained plenty of microsites suitable for colonization, indicating that species colonization and richness was limited by the rate of species dispersal. Indeed, consistent with these findings, our simulations showed that future metapopulation size greatly increased when using the high colonization rate resulting from propagule addition. As such, the long-term regional dynamics of the species in managed landscapes are restricted by low colonization rate, which is in turn restricted by both propagule dispersal range and establishment. This result supports the importance of restricted dispersal in determining metapopulation dynamics (Hanski 1999).

The model jointly estimating local and landscape-scale dispersal range (i.e., including two dispersal parameters) did not fit better than the model for mainly local dispersal, and led to similar conclusions regarding future metapopulation size. However, the tail of the dispersal kernel was slightly thicker. This suggests that *L. pulmonaria* dispersal in fragmented landscapes is mainly local with low probability of colonization on isolated trees. This agrees with the earlier finding of epiphyte colonization occurring close to the dispersal sources (Snäll et al. 2005a, Johansson et al. 2012, Ruete et al. 2014). For *L. pulmonaria*, similar restricted dispersal range of clonal

diaspores has been reported at the local scale (Walser et al. 2001, Walser 2004), although Werth et al. (2006) indeed also found long-distance dispersal. Gjerde et al. (2012, 2015) also found evidence for rare long-distance dispersal events. In contrast, a recent population genetic study conducted in an old-growth landscape suggests frequent long-distance dispersal as a result of abundant spore production (C. Ronnäs et al., *unpublished data*). Our model predicts both limited local dispersal and rare long-distance dispersal, but the restricted dispersal nevertheless limits the future metapopulation size in these fragmented landscapes. Moreover, the colonization probability increased with tree inclination, as found previously (Snäll et al. 2005a, Fedrowitz et al. 2012). This positive effect is probably explained by the decreasing risk for diaspore flush-off on leaning trees.

Local habitat conditions were a major determinant for the establishment success of *L. pulmonaria* and played a major role in subsequent population growth. Specifically, our results extend those from experimental seed addition studies in the ability to distinguish the influence of dispersal from that of environmental control. Although adding propagules greatly increased recruitment, not all trees were equally suitable for *L. pulmonaria* establishment. No experimental establishments took place on trees on clearcuts, and in closed stands the probability was lower on mesic and dry than on moist soils. Establishment thus did not take place due to post-dispersal environmental filtering, which occurs before colonization (Peterson and Pickett 1990, Clark et al. 2013). The trade-off between light and humidity plays a critical role during lichen establishment (Nash 2008). It is unlikely that exposure to high irradiance levels is a limitation in these boreal forests, but rather that establishment is limited by moisture availability at the tree scale. Increased light intensity leads to major concurring reductions in humidity and is detrimental for *L. pulmonaria* in the air-dry state (Gauslaa and Solhaug 1996, 1999). This is especially crucial during lichen establishment, as water storage capacity of juvenile thalli is low (Larsson et al. 2012). Moreover, fast attachment of propagules requires suitable abiotic conditions (Honegger 1993, 1996, Scheidegger and Werth 2009). If attachment is too slow, there is increased risk that the propagules are flushed off from the bark surface (Scheidegger et al. 1995, Hilmo and Sæstad 2001). The latter probably explains the positive effect of the depth of bark crevices on local population growth.

In our study system, local extinctions were driven by patch destruction and thus stochastic extinctions were negligible for long-term metapopulation dynamics. Setting the local stochastic extinction rate to zero in the projections resulted in no difference in the future metapopulation size compared to the scenario that used the mean extinction rate. This agrees with the “patch-tracking metapopulation” concept, which states that when a species has colonized a patch it is unlikely to go extinct until the patch disappears (Snäll et al. 2003).

However, empirical studies have also shown intermediate extinction dynamics in sessile organisms, i.e., both stochastic and deterministic extinctions (Laube and Zotz 2007, Caruso et al. 2010, Öckinger and Nilsson 2010, Fedrowitz et al. 2012, Zartman et al. 2012). For instance, Öckinger and Nilsson (2010) reported shorter local *L. pulmonaria* population longevities than the estimated longevity of the long-lived trees of formerly grazed areas that had developed into secondary woodlands. They argued that tree mortality was not an important driver of *L. pulmonaria* dynamics, suggesting that the main causes of extinctions were stochastic events or tree logging. Our results contrast their findings as the extinction rate resulting from tree death or fall was higher (13.7%) than that from cutting (9.9%) over a 10-yr period, and stochastic extinctions were negligible. These differences may be due to (1) light availability limiting population viability in the southern Swedish productive secondary woodlands with dense canopies, that Öckinger and Nilsson studied, (2) non-negligible stochastic extinction rates on at least a subset of the nemoral forest tree species they studied, or (3) the influence of non-detection of species occurrence on their estimate of extinction rate (presumably lower detectability than estimated in our study). If the latter explanation is not the main reason for the different results, then local stochastic extinctions of *L. pulmonaria* can be assumed to be negligible in boreal (studied here) but not in nemoral forest.

Our simulations predicted that the tree rotation length and the spatial placement of newly regenerated trees have large effects on future metapopulation size. The metapopulation size was projected to dramatically decrease with short tree rotation length. This confirms theoretical work showing that high rates of patch destruction may not be compensated by patch creation (Johst et al. 2011). The destruction of (occupied) patches not only directly reduces the metapopulation size but also the colonization rate due to reduced connectivity (Hanski 1999). Hence, the future metapopulation size is sensitive to the rate of patch destruction, regardless of the amount of habitat (Wilcox et al. 2006, Johst et al. 2011). The scenario with random placement of regenerated trees, considering both long and short rotation length, predicted a lower metapopulation size compared to maintained host tree aggregation. This supports the suggestion that increasing the degree of patch aggregation increases the colonization rate of species with poor dispersal abilities (Hanski 2000, Ovaskainen and Hanski 2001). Thus, our results make it clear that decreasing the tree rotation length from 120 to 65 yr will require a higher tree density and connectivity (short distance to occupied trees) to maintain a viable metapopulation.

Our study clarifies the importance of the key processes affecting the colonization and extinction dynamics of the well-studied model species *L. pulmonaria* in the long term. We demonstrated the large importance of restricted dispersal range and propagule availability, but also of local habitat conditions in driving establishment success

and subsequent local population growth. We showed that tree fall was the main operating process behind the local extinction rate. In addition, our work demonstrated the effect of tree rotation length and spatial aggregation on future metapopulation size. Although these findings do not mean we have answered all questions regarding metapopulation dynamics in dynamic landscapes, they emphasize the importance of applying a landscape-scale perspective to the management of both metapopulations of sessile species and the landscapes they inhabit.

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